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Road noise causes earlier predator detection and flight response in a free-ranging mammal

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Increasing scientific evidence shows that anthropogenic noise can impact behavioral, demographic and community-level processes across a range of taxa – presenting a serious

conservation challenge. Given the direct link between antipredator behavior and fitness, it is important to explore the impacts of noise on vigilance and flight. To do this, we conducted playback experiments to to test whether noise distracts black-tailed prairie dogs from attending to an approaching predator or whether increased noise exposure led to heightened vigilance and responsiveness. Contrary to the 'distracted prey hypothesis', prairie dogs responded at greater distances to the approaching human "predator" and took flight more rapidly in noise than during the quieter control. Greater vigilance is likely to be a function of increased perceived threat as opposed to distraction, enabling the prairie dogs to evade predators sooner. However, there are energetic and potential fitness costs associated with heightened vigilance and flight, including the loss of foraging opportunities. Interestingly the reactiveness of the prairie dogs to the approaching observer increased over the course of the study, but there was no apparent change in their responses to other humans using the natural area. This may reflect their impressive cognitive abilities that enable discrimination between different predators – even human observers. Our findings emphasize that the complex biological responses to anthropogenic noise are dependent upon the biology of the species as well as the acoustic characteristics of the noise source.

Key words: anthropogenic disturbance, vigilance, predation, playback, environmental change

INTRODUCTION

Over the past decade, the effects of rising global anthropogenic noise levels on wildlife have received increasing attention from the scientific community (Shannon et al. 2016). Research has demonstrated that noise affects a range of species across the major taxonomic groups in both terrestrial and aquatic environments. The responses range from altered behavior and physiology

of the individual to effects at the population and community level mediated by changes in densities and abundance (Barber et al. 2010; Francis and Barber 2013; Shannon et al. 2016). This presents a pressing challenge for biodiversity conservation (McGregor et al. 2013), particularly given that increasing noise levels are so closely tied to human population growth and development.

Evidence concerning the impacts of anthropogenic noise is mounting, with a large number of studies demonstrating impacts of noise on acoustic communication, physiology and movement (particularly in birds and marine mammals; Shannon et al. 2016). Noise may also have important effects on predator-prey interactions. In addition to removing prey animals from the population, predators can indirectly alter behavior and reproductive success as a function of perceived risk (Creel et al. 2007; Zanette et al. 2011). Antipredator behavior is therefore directly linked to fitness and provides a useful metric in terms of the costs associated with noise exposure. Indeed, a significant challenge of noise research has been to translate the short-term behavioral responses into population-level effects, particularly as animals may exhibit behavioral flexibility (e.g. foraging, vocal communication) to compensate for noise exposure. However, if predator detection is compromised, this will directly impact the survival probability of the animals concerned (Simpson et al. 2016).

Noise can affect the behavior of prey species in three distinct ways, including distracting animals from detecting an approaching predator (Chan and Blumstein 2011; Blumstein 2013), reducing auditory surveillance by masking the sounds of an approaching predator (Barber et al. 2010), or by directly being perceived as a threat (Quinn *et al.*, 2006; Meillere, Brischoux & Angelier, 2015). The distracted prey hypothesis is perhaps the least explored possibility, though there is some evidence for noise-induced distraction in crustaceans (Chan et al. 2010a,b; Wale et al. 2013) and fish (Simpson et al. 2015), but see (Voellmy et al. 2014). The hypothesis is based

on the finite attention and information processing capability of an animal. Anthropogenic noise generates an extra peripheral stimulus that can potentially distract the animal from attending to crucial cues in the environment. This effect was clearly demonstrated in wild Caribbean hermit crabs (*Coenobita clypeatus*), with a simulated predator able to approach closer in noise before the crabs took evasive action (Chan et al. 2010a). Despite these interesting findings, there has been only limited exploration of the distracted prey hypothesis outside of the lab.

Our recent research demonstrated that traffic noise altered the aboveground activity of black-tailed prairie dogs (*Cynomys ludovicianus*; hereon referred to as prairie dogs), which included an increase in their alert behavior (Shannon et al. 2014), concurring with research on Californian ground squirrels (*Spermophilus beecheyi*) (Rabin et al. 2006). We wanted to now explicitly test whether noise affects the ability of these highly social animals to detect and take flight from an approaching predator. If prairie dogs behave according to the distracted prey hypothesis (Chan et al. 2010, a,b), we predicted that exposure to noise would distract the finite attention of the prairie dogs, delaying the detection of and flight from an approaching predator, relative to a control period without noise. Alternatively, heightened predator detection could be driven by the increased perceived threat associated with noise (risk disturbance hypothesis: Frid & Dill, 2002), or indirectly by noise masking the transmission of conspecific alarm calls and/or auditory predator cues (Barber et al. 2010). Under these conditions perceived risk would likely be elevated and increased investment in visual scanning of their surroundings could allow earlier detection and flight from an approaching predator (flush early and avoid the rush hypothesis: Blumstein 2010).

METHODS

Study Site

The research was conducted in the Pineridge Natural Area (250 hectares), located on the western boundary of Fort Collins, Colorado. The predominant habitat is shortgrass prairie, which is home to a contiguous population of prairie dogs that extends 2.5km from North to South and varies in width between 100-350m from East to West. The population was divided into three discrete study colonies (East, West and South) that were separated by at least 50m. Pineridge has a well-developed trail network that is used by walkers, runners and cyclists. The prairie dogs are therefore accustomed to human activity. However, with only a small county road on the northwest boundary, road noise exposure is minimal. Detailed weather data were available from a nearby weather station at Colorado State University.

Experimental approach

62 experiments (31 noise exposures and 31 controls) were conducted across the three study colonies from 8 October - 8 November 2014, with each colony only sampled once per week (4-7 experiments per sampling period). The observer (GS) stood on a walking trail near colony and randomly selected an individual prairie dog that was engaged in foraging and not vigilant or paying attention to the observer. The colonies were comparatively large and continuous in extent, so the number of animals within a radius of 10m of the focal individual were counted (mean ± s.e = 2.3 ± 0.2 individuals). A remote-controlled speaker was placed directly in line with the animal perpendicular to the walking trail. Prior to the start of the experiment, the observer then moved 30m further along the trail so that the 'predator' approach would be at an angle of approximately 30-45° relative to the speaker (see Figure 1). The distance to the prairie dog was measured using a laser rangefinder (start distance, 35-65m). Once it was confirmed that the target prairie dog remained relaxed and there was no alarm calling or agitation from animals in the immediate

vicinity, the observer moved toward the target animal at a consistent speed of 0.5m/s (following the protocol in Blumstein et al. 2004). The speed was standardized using pre-experimental training to ensure that a test 'walk' of 20m on the day of each experiment fell within 95% accuracy (i.e. 38-42 seconds). A first beanbag was dropped when the prairie dog became alert to the presence of the 'predator' and a second was dropped when the prairie dog took flight. Flight was defined as movement away from the predator – this was generally in the direction of the nearest burrow. The laser range finder was used to measure the distance from each beanbag to the observer's starting position to determine the alert distance and flight initiation distance.

Experiments were alternated between control (no noise) and treatment, which involved the broadcast of road noise from the remote-controlled speaker (62dBA Leq at 10m). The road noise was recorded along Interstate 25, 16km South of Fort Collins (see Shannon et al. 2014 for further details). The playback of road noise was initiated using a remote control 2 minutes before the predator approach was initiated. The ambient sound levels were recorded after each experiment (mean = 33 dBA Leq), while the received noise levels were recorded at the end of the treatment (mean = 43 dBA Leq). Prior to each predator approach, the position of the focal animal was noted so that these recordings could be carried out at that same location after the experiment to determine the specific ambient and received sound levels. All sound level measurements were made using a calibrated sound level meter (Larson-Davis 831).

Data analysis

140 The data were analyzed in a generalized linear mixed model (GLMM) framework using the nlme
141 package in R (R Core Development Team 2012), while Akaike's Information Criterion adjusted
142 for small sample size (AICc) was used for model selection (Burnham and Anderson 2002). It was
143 necessary to use a corrected measure for the flight variable, because the maximum distance that
144 an animal can take flight is constrained by the distance that it becomes alert to an approaching
145 predator, which could potentially bias the analysis. We therefore also calculated a 'corrected
146 flight distance', which was the difference between the alert distance and the flight distance (lower
147 values indicate more rapid flight response).
148 The identity of the colony was included as a random effect due to the repeated sampling
149 design. Eleven candidate models were generated *a priori* for each response variable (alert
150 distance and corrected flight distance) based on several predictors: *exposure* (treatment vs.
151 control) to test for behavioral differences with and without road noise; *Julian day* and *decimal*
152 *time*, to determine whether behavioral response changed temporally; *ambient sound* to explore if
153 background sound levels affect response; distance to the *nearest individual* to establish if the
154 proximity of conspecifics changes behavior and *start distance* to account for the variation
155 between experiments (Table S1 – electronic supplementary material). Temperature was initially
156 included in the models as it has been shown to influence prairie dog activity (Shannon et al.
157 2014). However, it was removed from the final analyses due to the strong correlation with Julian
158 day and decimal time. Further exploration of the data also revealed that temperature did not play
159 a role in explaining the alert or flight responses of the prairie dogs. An interaction explored
160 whether behavioral response to noise exposure versus the control changed in relation to the
161 starting position (*start distance*) of the observer. The AICcmodavg package was used to extract
162 AICc scores and model weights for candidate models of each response variable. Model averaging
163 was conducted on the response specific models accounting for ≥0.95 of the AICc weight to

extract parameter β-estimates and their 95% confidence intervals. The effect sizes were assessed by whether the 95% confidence intervals overlapped zero.

RESULTS

The observer was able to approach closer to the target animal during control experiments compared with the noise exposure experiments, with average alert and flight initiation distances of 37m and 32m respectively during the control experiments, compared to 41m and 37m for the treatment experiments (Figure 2a). The mean starting distance was the same for both the control and treatment (47m), allowing for direct comparison (Figure 2a). Corrected flight distances demonstrated that prairie dogs took flight more rapidly after detecting the approaching predator during noise exposure compared with the quieter control (Figure 2b).

Nine models contributed 95% of the AICc weight for the alert behavior GLMM analysis (Table 1), with the top three models accounting for 54% of the weight. Model averaging revealed that exposure to traffic noise was a key predictive explanatory variable (Table 2), with alert distances greater during the playbacks of noise. The only other important predictor variable was starting distance with a positive effect indicating that the greater the distance at which the observer initiated the approach, the greater the alert distance.

The analysis of the corrected flight data (the distance between the animal becoming alert and taking flight) generated 9 top models, with the top three accounting for 56% of the AICc weight (Table 1). Exposure was again a key parameter (Table 2), with more rapid flight in the noise treatment than during the control. As with alert behavior, start distance appeared to be positively correlated with corrected flight distance, but the relationship was relatively weak with the 95% confidence intervals marginally overlapping zero. Julian day was also an important

parameter in the analysis, with a negative relationship indicating that the subjects took flight sooner as the experiments progressed. Indeed, the decline in corrected flight distances across both the control and treatment periods could be predicted with a relatively high degree of precision using the best model (Figure 3).

DISCUSSION

Contrary to the distracted prey hypothesis (Chan and Blumstein 2011; Blumstein 2013), prairie dogs became alert and took flight earlier when a simulated predator approached during experimental noise exposure. These results and our previous research (Shannon et al. 2014) suggest that the introduction of a novel acoustical stimulus increases focused vigilance and predator detection, rather than causing distraction, concurring with the risk disturbance hypothesis (Frid and Dill 2002). To our knowledge, this study provides the first detailed test of the distracted prey hypothesis in a mammal – free ranging or otherwise. It also further emphasizes the complex biological responses driven by noise exposure, which are dependent upon the biology of the focal species (e.g. behavioral state, cognition, sociality, trophic level, hearing range, vocal behavior) (Ellison et al., 2012; Francis & Barber, 2013; Shannon et al., 2016). Indeed, a number of crustaceans and fish species have demonstrated marked distraction and impaired antipredator behavior when exposed to anthropogenic noise under both natural and laboratory conditions (Chan et al. 2010a,b; Wale et al. 2013, Simpson et al. 2015). A recent study on damselfish, which combined field and laboratory experiments demonstrated for the first time that exposure to noise not only changed antipredator behavior, but directly resulted in greater mortality due to increased predation (Simpson et al. 2016).

Although prairie dogs are still capable of detecting and responding to an approaching predator under noisy conditions, they also demonstrate that greater vigilance causes animals to be more reactive and take flight earlier. These findings fit with the flush early and avoid the rush hypothesis, which predicts that animals will take flight soon after detection of a potential predator so as to limit the attentional costs of continued surveillance (Blumstein 2010; Samia et al. 2013). Nevertheless, such a response – which is likely further exacerbated by the increased perceived risk associated with noise – may result in increased energetic costs associated with flight and lost foraging opportunities (Preisser et al. 2005), particularly when the approaching threat is relatively benign. Our results also concur with a recent study on nesting sparrows, which demonstrated that females exposed to noise flushed from nests sooner than individuals in ambient conditions, which could impact nestling development (Meillere et al. 2015).

Acoustical masking of an approaching predator has been proposed as a mechanism to explain increased vigilance (Barber et al. 2010), and the perception of reduced auditory detection may have increased prairie dog vigilance during our noise treatments. However, acoustic masking did not appear to reduce the actual detection of the "predator" in our study, particularly as approaches were conducted quietly at distances of ≥35m. Indeed, hearing may not play a major role in the detection of natural predators in this open habitat where vision is primarily used to detect stealthy predators (e.g. coyotes, eagles). However, it is also important to consider that acoustical masking may also reduce the signaling distance of conspecific vocalizations (e.g. alarm calls) during exposure to noise, which has been shown to alter behavior and even demography in a range of taxa (Shannon et al. 2016).

Over the course of the study, the prairie dogs appeared to become sensitized and more reactive to the approaching predator during both the control and treatment experiments. In fact, in situations where non-target prairie dogs were foraging in close proximity (<15m) to the pathway,

233 the observer found it increasingly challenging to pass by without eliciting vigilance and alarm
234 calls. Interestingly, this reaction appeared to be targeted specifically at the observer, while
235 passing hikers, runners and cyclists were largely ignored. Previous research has demonstrated
236 that prairie dogs can discriminate between different predators and human observers, labelling
237 them with distinct alarm calls (Slobodchikoff et al. 1991; Kiriazis and Slobodchikoff 2006;
238 Slobodchikoff and Placer 2006; Slobodchikoff et al. 2009). Furthermore, prairie dogs exhibited
239 increased reactivity, not habituation, in experiments that involved repeated human intrusion on a
240 colony (Magle et al. 2005). It is also important to reiterate, that despite evidence of overall
241 increased sensitization to the approach of the observer, predator detection and flight was
242 consistently more rapid during noise exposure experiments throughout the study.
243 Longer-term experiments are required to determine whether continued exposure to noise
244 would ultimately result in habituation. It is important to note that just because a species inhabits a
245 noisy area does not mean it has habituated to the disturbance or is immune to its costs (Francis
246 and Barber 2013). Prairie dogs are a prime example of a species found in habitats close to human
247 habitation and infrastructure, but this may be a consequence of rapid human development and the
248 challenge of an entire colony relocating, rather than tolerance of human presence. Indeed, prairie
249 dog populations have declined dramatically over the past 100 years as a result of habitat loss and
250 fragmentation (Miller et al. 1994). The costs of external stressors such as noise may well
251 exacerbate the vulnerability of remaining prairie dog colonies to other heterotypic environmental
252 stressors (e.g. disease, habitat fragmentation, human activity).
253 Our findings demonstrate the ability of prairie dogs to identify the threat of an
254 approaching predator in anthropogenic noise without becoming distracted like other species
255 (Chan et al. 2010a; Wale et al. 2013; Simpson et al. 2015). Nonetheless, greater vigilance and
256 responsiveness due to chronic noise exposure can be costly behaviors that may have potential

257 energetic and fitness consequences at the population level. Future investigation is required to
258 understand how antipredator behavior is affected by fluctuating sound levels at sites that
259 experience chronic anthropogenic noise exposure (e.g. urban prairie dog populations), as well as
260 contrasting the effects of anthropogenic noise on alert and flight initiation distances with natural
261 sounds (e.g. wind). It would also be interesting to determine if the detection of predator
262 vocalizations and conspecific alarm calls would be masked in the presence of noise, and if so,
263 whether prairie dogs use vocal adjustments (e.g. change in pitch and/or frequency shown by a
264 number of urban bird species: Slabbekoorn 2013) to mitigate potential acoustical masking in
265 noisy areas.
266
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272
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346 Table 1. Top models of prairie dog (a) alert distance and (b) corrected flight distance accounting
347 for ≥0.95 of the AICc weight. All models include the identity of the colony as a random effect.
348 Parameters in the interaction terms are also included in the model additively.
349

	K[1]	ΔAICc	AICc weight
a) Alert Distance			
Exposure + Start Distance + Julian Day	6	0.00	0.22
Exposure + Start Distance	5	0.04	0.22
Exposure * Start Distance	6	1.58	0.10
Exposure + Start Distance + Nearest Individual	6	1.79	0.09
Exposure + Start Distance + Julian Day + Nearest Individual	7	1.85	0.09
Exposure + Start Distance + Time	6	2.30	0.07
Exposure + Start Distance + Ambient Sound	6	2.48	0.06
Exposure + Start Distance + Julian Day + Time	7	2.53	0.06
Exposure + Start Distance + Julian Day + Ambient Sound	7	2.53	0.06
b) Flight Distance (corrected)			
Exposure + Start Distance + Julian Day	6	0.00	0.30
Exposure + Start Distance + Julian Day + Nearest Individual	7	1.45	0.14
Exposure + Start Distance + Julian Day + Time	7	1.74	0.12
Exposure + Start Distance	5	2.31	0.09
Exposure + Start Distance + Julian Day + Ambient Sound	7	2.40	0.09
Exposure * Start Distance	6	2.48	0.09
Exposure + Start Distance + Nearest Individual	6	3.69	0.05
Exposure + Start Distance + Julian Day + Ambient Sound + Nearest Individual	8	3.70	0.05
Exposure + Start Distance + Ambient Sound	6	4.26	0.04

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Table 2. The observed relationship between each response variable and the model-averaged parameters from the top models (β-estimate ±95% CI). Bold text denotes β-estimates with 95% CI that do not overlap zero.

	Parameter	β Estimate	(95% CI)
Alert Distance	Exposure	**3.95**	**(2.13 / 5.77)**
	Julian day	0.08	(-0.02 / 0.18)
	Time	-0.06	(-0.79 / 0.67)
	Ambient sound level	0.00	(-0.34 / 0.34)
	Nearest Individual	-0.10	(-0.32 / 0.13)
	Start Distance	**0.83**	**(0.72 / 0.94)**
	Exposure * Start Distance	0.11	(-0.11 / 0.32)
Flight Distance (corrected)	Exposure	**-1.72**	**(-2.97 / -0.47)**
	Julian day	**-0.08**	**(-0.15 /-0.01)**
	Time	-0.18	(-0.70 / 0.33)
	Ambient sound level	0.07	(-0.16 / 0.30)
	Nearest Individual	0.08	(-0.07 / 0.24)
	Start Distance	0.07	(-0.01 / 0.15)
	Exposure * Start Distance	-0.12	(-0.26 / 0.03)

366 Figure 1. Experimental setup used at the three prairie dog colonies in Pineridge Natural Area,
367 Fort Collins, Colorado.
368
369 Figure 2. Prairie dog responses to predator approach. (a) The mean (± SE) observer start distance,
370 and alert and flight initiation distances of the target prairie dog during the road noise treatment
371 and control experiments. (b) The mean (± SE) corrected flight distance (distance for the target
372 animal to take flight after becoming alert to the approaching predator) for the road noise
373 treatment and control experiments.
374
375 Figure 3. Corrected flight distances predicted for the entire 31-day study period using the best
376 model. The shaded areas show the 95% confidence intervals with the darkest shading indicating
377 areas of overlap.
378
379